

THE MUSSELS (MOLLUSCA: BIVALVIA: UNIONIDAE) OF TENNESSEE

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ABSTRACT

The unionid fauna that occurs within the political boundaries of the State of Tennessee is reviewed. The fauna reported from the Tennessee, Cumberland, Conasauga and Mississippi river drainages is compared and discussed. There are 155 unionid taxa (species and subspecies) that currently occur or that have been reported historically from the state.

The State of Tennessee, because of the physiographic diversity and discrete drainages encompassed by its boundaries, has one of the most diverse mussel faunas in North America. The state's molluscan fauna is enriched by virtue of having four major river drainages: Mississippi, Tennessee, Cumberland and Conasauga (Coosa River system) (Fig. 1). Bickel (1968) listed 133 unionid taxa from Tennessee but included only the fauna from the Tennessee and Cumberland rivers. A total of 155 taxa have now been recorded from the state. While the unionid fauna from the Tennessee and Cumberland rivers has been historically documented and periodically evaluated, the unionid fauna from the Mississippi River and its direct tributaries in Tennessee, as well as the Conasauga River, has only recently been described.

The vast majority of the unionid fauna is associated with big river habitat. Pollution, channelization, commercial harvest, impoundments and other modifications, have greatly reduced the extent of suitable riverine habitat, curtailing distribution of many species. Of the 24 unionid species listed by the U. S. Fish and Wildlife Service as threatened or endangered, 18 (75%) occur in Tennessee (Hatcher and Ahlstedt, 1982; Bogan and Parmalee, 1983). Most of these species are endemic to the Tennessee and Cumberland rivers (Table 1).

This presentation reviews literature, archaeological and unpublished museum records of the unionid fauna in the State of Tennessee. An in depth analysis of each Tennessee unionid

species that involves taxonomy, shell description, distribution and related data is currently under preparation by Dr. Paul W. Parmalee, McClung Museum, University of Tennessee, Knoxville.

RELEVANT FAUNAL STUDIES

Of the four major river drainages, the Tennessee River unionid fauna is the most thoroughly studied. Pilsbry and Rhoads (1897), Coker and Boepple (1912), Ortmann (1918), Brown and Pardue (1980), Pardue (1981) and Dennis (1984) described the unionid fauna in the upper Tennessee River tributaries. Parmalee and Klippel (1984) documented the fauna of the Tellico River, a tributary to the Little Tennessee River. Bogan and Starnes (1983) discussed the Little River unionid fauna. Hickman (1937) surveyed the Clinch River below Norris Dam, prior to the dam's completion. Bates and Dennis (1978) and Ahlstedt (1984) discussed the current status of the unionid fauna of the Clinch River. Dennis (1981) summarized some early historical and certain recent unionid data for the Powell River. Ortmann (1925) described the fauna of the Tennessee River and its tributaries in northern Alabama and southern Tennessee. Isom (1972) reported the freshwater bivalve fauna at the Nickajack Dam Site. Ortmann (1924) described the fauna of the Duck River. Subsequently, van der Schalie (1939, 1973), Isom and Yokley (1968) and Ahlstedt (1981) documented drastic declines in the mussel fauna of the Duck River. The Elk River was surveyed by Remington

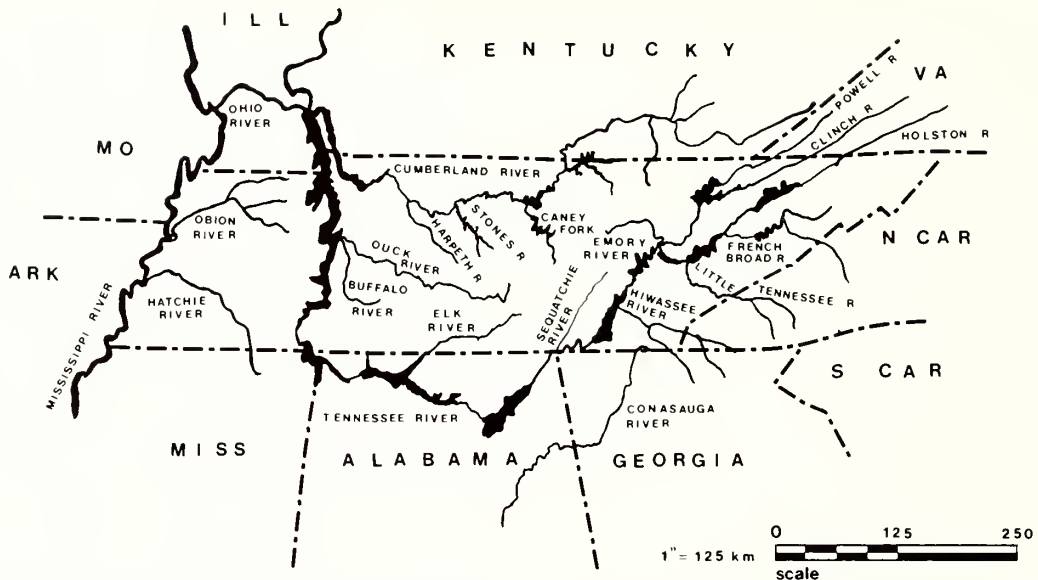


Fig. 1. Map showing the major tributary rivers to the Cumberland, Tennessee and Mississippi rivers in the State of Tennessee.

and Clench (1925), Ortmann (1925), Isom *et al.* (1973) and Ahlstedt (1983). Isom (1969) compared mussel faunas collected in 1965 from the Tennessee River with those recorded prior to impoundment. Scruggs (1960) and Isom and Gooch (1986) made similar pre and post-impoundment comparisons. Yokley (1972) compared the ecology and stocks of species in Kentucky Reservoir. The Tennessee Valley Authority (TVA) Cumberlandian Mollusk Conservation Program, detailed collections from the Clinch, Powell, Nolichucky, Holston, Elk, Duck and Buffalo rivers (Ahlstedt, 1986).

Unionids of the Cumberland River system in Tennessee were studied by Wilson and Clark (1914), Neel and Allen (1964), Isom *et al.* (1979), Parmalee *et al.* (1980), Clarke (1981, 1985), Call and Parmalee (1982), Schmidt (1982), Sickel (1982), Starnes and Bogan (1982) and Stansbery *et al.* (1983). The fauna in the Cumberland River appears similar to that of the Tennessee River, but has not been as thoroughly surveyed and future work could uncover significant differences.

Of the 87 mussel taxa recorded from the Tennessee River, the 69 taxa recorded from the Duck River, and the 78 taxa recorded from the Cumberland River, Ortmann (1924) considered 45 of these to be unique to the Tennessee and Cumberland rivers and referred to them as "Cumberlandian". Ortmann (1925) defined the downriver limits of the Cumberlandian fauna to be Clarksville, Tennessee, on the Cumberland River; Muscle Shoals, Alabama, on the Tennessee River; and between Columbia and Centerville on the Duck River. Below these limits, Interior Basin molluscan species replaced the Cumberlandian species. Ortmann later liberalized these limits, suggesting that some Cumberlandian species had emigrated into the Ohio River as well as into the Interior Basin.

Reports of unionids from the Mississippi River tributaries in Tennessee have been limited to Ortmann (1926a) and van der Schalie and van der Schalie (1950). Recent collections from the Hatchie River (D. Manning, pers. comm.)

suggest a diverse fauna. With the exception of the Hatchie River, direct Mississippi River tributaries in Tennessee have suffered extensive channelization resulting in major alterations of their biological communities and a significant reduction of the unionid fauna.

The mussel fauna of the Conasauga River located in the southeast corner of Tennessee is relatively unknown with Hurd (1974), van der Schalie (1981) and museum records providing the only information on this northern Coosa River tributary.

TAXONOMY

Table 1 lists unionid taxa found in the Tennessee and Cumberland rivers in Tennessee. A comparison is made of the nomenclature used by Bickel (1968) and Morrison (1970) with the names used in this paper (Table 1). The American Malacological Union List of Common and Scientific Names [Turgeon *et al.* (in press)] is incorporated as the basis for the taxonomy used in this paper. However, the status of many named subspecific varieties and ecophenotypes has not been resolved. We list them here for clarity. Since the report by Bickel (1968), almost half of the taxa have undergone taxonomic revision. Morrison (1970) and Johnson (1978) declared *Plagiola* Rafinesque, 1819 available over *Dysnomia* Agassiz, 1852, but due to taxonomic questions about the type species, we have chosen to use *Epioblasma* Rafinesque, 1831, the next available generic name. Similarly, the change from *Carunculina* Simpson in Baker, 1898 to *Toxolasma* Rafinesque, 1831 involves five taxa (see Bogan and Parmalee, 1983). Additionally, 12 taxa have been added to the state's total list of species while two, *Fusconaia undata*, (Barnes, 1823) and *Amblema peruviana* (Lamarck, 1819) have been synonymized.

Bickel (1968) used 25 taxa originally described by Rafinesque. Morrison (1970) included 26 nomenclatural changes based on the priority of Rafinesque descriptions. In

Table 1. List of Tennessee unionids found in the Tennessee/Cumberland river systems.

Bickel (1968)	Morrison (1969)	Taxonomy used in this study
<i>Actinonaias carinata</i> (Barnes, 1823)	<i>Actinonaias ligamentina</i> (Lamarck, 1819)	<i>Actinonaias ligamentina</i>
<i>A. carinata gibba</i> (Simpson, 1900)		<i>A. ligamentina gibba</i>
<i>A. pectorosa</i> (Conrad, 1834)		<i>A. pectorosa</i>
<i>Alasmidonta marginata</i> Say, 1819		<i>Alasmidonta atropurpura</i> (Raf., 1831)
		<i>A. marginata</i>
<i>A. minor</i> (Lea, 1845)	<i>Alasmidonta viridis</i> (Rafinesque, 1820)	<i>A. raveneliana</i> (Lea, 1834)
<i>Amblema costata</i> (Rafinesque, 1820)		<i>A. viridis</i>
<i>A. costata perplicata</i> (Conrad, 1841)		<i>Amblema plicata</i> (Say, 1817)
<i>A. costata plicata</i> (Say, 1817)		<i>A. plicata perplicata</i>
<i>A. peruviana</i> (Lamarck, 1819)		<i>A. plicata plicata</i> (Say, 1817)
<i>Anodonta grandis</i> Say, 1829		<i>A. plicata plicata</i>
		<i>Anodonta grandis grandis</i>
<i>A. grandis gigantea</i> Lea, 1838		<i>A. grandis corpulenta</i> Cooper, 1834
<i>A. imbecillis</i> Say, 1829		<i>A. grandis grandis</i>
<i>A. suborbiculata</i> Say, 1831		<i>A. imbecillis</i>
<i>Anodontoides ferussacianus</i> (Lea, 1834)		<i>A. suborbiculata</i>
<i>Arcidens confragosus</i> (Say, 1829)		<i>Anodontoides ferussacianus</i>
<i>Carunculina glans</i> (Lea, 1831)	<i>Toxolasma livida</i> Rafinesque, 1831	<i>Arcidens confragosus</i>
		<i>Toxolasma lividus glans</i>
<i>C. moesta</i> (Lea, 1841)		<i>T. lividus lividus</i>
<i>C. moesta cylindrella</i> (Lea, 1868)		<i>T. lividus glans</i>
<i>C. parva</i> (Barnes, 1823)		<i>T. cylindrella</i>
<i>C. texasensis</i> (Lea, 1857)		<i>T. parva</i>
<i>Conradilla caelata</i> (Conrad, 1834)	<i>Lemiox rimosus</i> Rafinesque, 1831	<i>T. texasensis</i>
<i>Cumberlandia monodonta</i> (Say, 1829)		<i>Lemiox rimosus</i>
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)		<i>Cumberlandia monodonta</i>
<i>C. tuberculata granifera</i> (Lea, 1838)		<i>Cyclonaias tuberculata tuberculata</i>
<i>Cyprogenia irrorata</i> (Lea, 1830)	<i>Cyprogenia stegaria</i> (Rafinesque, 1820)	<i>C. tuberculata granifera</i>
<i>Dromus dromas</i> (Lea, 1834)		<i>Cyprogenia stegaria</i>
<i>D. dromas caperatus</i> (Lea, 1845)		<i>Dromus dromas dromas</i>
<i>Dynomia arcaeformis</i> (Lea, 1831)		<i>D. dromas caperatus</i>
		<i>Epioblasma arcaeformis</i>
<i>D. brevidens</i> (Lea, 1831)	<i>Plagiola interrupta</i> (Rafinesque, 1820)	<i>E. biemarginata</i> (Lea, 1857)
<i>D. capsaeformis</i> (Lea, 1834)		<i>E. brevidens</i>
<i>D. flexuosa</i> (Rafinesque, 1820)		<i>E. capsaeformis</i>
<i>D. florentina</i> (Lea, 1857)		<i>E. flexuosa</i>
<i>D. florentina walkeri</i> (Wilson and Clark, 1914)		<i>E. florentina florentina</i>
<i>D. haysiana</i> (Lea, 1833)		<i>E. florentina walkeri</i>
<i>D. lenior</i> (Lea, 1842)		<i>E. haysiana</i>
<i>D. lewisi</i> (Walker, 1910)		<i>E. lenior</i>
<i>D. stewardsoni</i> (Lea, 1852)		<i>E. lewisi</i>
		<i>E. stewardsoni</i>
<i>D. torulosa</i> (Rafinesque, 1820)		<i>E. obliquata</i> (Raf., 1820)
		(= <i>sulcata</i> Lea, 1829)
<i>D. torulosa gubernaculum</i> (Reeve, 1865)		<i>E. torulosa</i>
<i>D. torulosa propinqua</i> (Lea, 1857)		<i>E. torulosa cincinnatiensis</i> (Lea, 1840)
<i>D. triquetra</i> (Rafinesque, 1820)		<i>E. torulosa gubernaculum</i>
<i>D. turgida</i> (Lea, 1848)		<i>E. propinqua</i>
<i>Elliptio crassidens</i> (Lamarck, 1819)		<i>E. triquetra</i>
<i>E. dilatatus</i> (Rafinesque, 1820)		<i>E. turgidula</i>
<i>Fusconaia barnesiana barnesiana</i> (Lea, 1838)		<i>Elliptio crassidens</i>
<i>F. barnesiana bigbyensis</i> (Lea, 1841)		<i>E. dilatata</i>
<i>F. barnesiana tumescens</i> (Lea, 1845)		<i>Fusconaia barnesiana</i>
<i>F. cuneolus cuneolus</i> (Lea, 1840)		<i>F. barnesiana bigbyensis</i>
<i>F. cuneolus appressa</i> (Lea, 1871)		<i>F. barnesiana tumescens</i>
<i>F. ebena</i> (Lea, 1831)	<i>Fusconaia pusilla</i> (Rafinesque, 1820)	<i>F. cuneolus</i>
<i>F. edgariana</i> (Lea, 1840)		<i>F. cuneolus appressa</i>
<i>F. edgariana analoga</i> (Ortmann, 1918)		<i>F. ebena</i>
		<i>F. cor cor</i> (Conrad, 1834)
		<i>F. cor analoga</i>

Table 1. (continued)

Bickel (1968)	Morrison (1969)	Taxonomy used in this study
<i>F. flava</i> (Rafinesque, 1820)		<i>F. flava</i>
<i>F. subrotunda</i> (Lea, 1831)	<i>F. polita</i> Say, 1834	<i>F. subrotunda subrotunda</i>
<i>F. subrotunda leseuriana</i> (Lea, 1840)	<i>F. polita leseuriana</i>	<i>F. subrotunda leseuriana</i>
<i>F. subrotunda pilaris</i> (Lea, 1840)	<i>F. polita pilaris</i>	<i>F. subrotunda pilaris</i>
<i>F. undata</i> (Barnes, 1823)	<i>F. lateralis</i> (Rafinesque, 1820)	<i>F. flava</i>
<i>Lampsilis anodontooides</i> (Lea, 1831)	<i>Lampsilis teres</i> (Rafinesque, 1820)	<i>Lampsilis teres anodontooides</i>
<i>L. anodontooides fallaciosa</i> (Smith, 1899)		<i>L. teres teres</i>
<i>L. fasciola</i> Rafinesque, 1820		<i>L. fasciola</i>
<i>L. orbiculata</i> (Hildreth, 1828)	<i>L. abrupta</i> Say, 1831	<i>L. abrupta</i>
<i>L. ovata</i> (Say, 1817)		<i>L. ovata</i>
<i>L. ovata satura</i> (Lea, 1852)		<i>L. cardium satura</i>
<i>L. ovata ventricosa</i> (Barnes, 1832)	<i>L. cardium cardium</i> (Raf., 1820)	<i>L. cardium cardium</i>
		<i>L. siliquoida</i> (Barnes, 1823)
<i>L. virescens</i> (Lea, 1858)		<i>L. virescens</i>
<i>Lasmigona complanata</i> (Barnes, 1823)		<i>Lasmigona complanata</i>
<i>L. costata</i> (Rafinesque, 1820)		<i>L. costata</i>
<i>L. holstonia</i> (Lea, 1838)	<i>Lasmigona badia</i> (Rafinesque, 1831)	<i>L. holstonia</i>
<i>Lastena lata</i> (Rafinesque, 1820)		<i>Hemistena lata</i>
<i>Leptodea fragilis</i> (Rafinesque, 1820)		<i>Leptodea fragilis</i>
<i>L. leptodon</i> (Rafinesque, 1820)		<i>L. leptodon</i>
<i>Lexingtonia dolabelloides</i> (Lea, 1840)		<i>Lexingtonia dolabelloides</i>
<i>L. dolabelloides conradi</i> (Vanatta, 1915)		<i>L. dolabelloides conradi</i>
<i>Ligumia recta latissima</i> (Rafinesque, 1820)		<i>Ligumia recta latissima</i>
<i>L. subrostrata</i> (Say, 1831)		<i>L. subrostrata</i>
<i>Medionidus conradicus</i> (Lea, 1834)		<i>Medionidus conradicus</i>
<i>Megaloniaias gigantea</i> (Barnes, 1823)	<i>Megaloniaias nervosa</i> (Rafinesque, 1820)	<i>Megaloniaias nervosa</i>
<i>Obliquaria reflexa</i> (Rafinesque, 1820)		<i>Obliquaria reflexa</i>
<i>Obovaria olivaria</i> (Rafinesque, 1820)		<i>Obovaria olivaria</i>
<i>O. retusa</i> (Lamarck, 1819)		<i>O. retusa</i>
<i>O. subrotunda</i> (Rafinesque, 1820)		<i>O. subrotunda</i>
<i>O. subrotunda lens</i> (Lea, 1831)		<i>O. subrotunda lens</i>
<i>O. subrotunda levigata</i> (Rafinesque, 1820)		<i>O. subrotunda levigata</i>
<i>Pegias fabula</i> (Lea, 1838)		<i>Pegias fabula</i>
<i>Plagiola lineolata</i> (Rafinesque, 1820)		<i>Ellipsaria lineolata</i>
<i>Plethobasus cooperianus</i> (Lea, 1834)	<i>Plethobasus striatus</i> (Rafinesque, 1820)	<i>Plethobasus cooperianus</i>
	<i>P. pachosteus</i> (Raf., 1820)	<i>P. cicatricosus</i> (Say, 1829)
<i>P. cyphus</i> (Rafinesque, 1820)		<i>P. cyphus</i>
<i>P. cyphus compertus</i> (Frierson, 1911)		<i>P. cyphus compertus</i>
<i>Pleurobema aldrichianum</i> Goodrich, 1931		<i>Pleurobema aldrichianum</i>
<i>P. clava</i> (Lamarck, 1819)		<i>P. clava catillus</i>
<i>P. coccineum</i> (Conrad, 1836)		<i>P. coccineum</i>
<i>P. cordatum</i> (Rafinesque, 1820)	<i>Pleurobema obliquum</i> Lamarck, 1819	<i>P. cordatum</i>
		<i>P. gibberum</i>
<i>P. oviforme</i> (Conrad, 1834)		<i>P. oviforme</i>
<i>P. oviforme argenteum</i> (Lea, 1841)		<i>P. oviforme argenteum</i>
<i>P. oviforme holstonense</i> (Lea, 1840)		<i>P. oviforme holstonense</i>
<i>P. pyramidatum</i> (Lea, 1831)	<i>P. obliquata</i> Rafinesque, 1820	<i>P. rubrum</i> (Rafinesque, 1820)
	<i>P. permorsa</i> Rafinesque, 1831	<i>P. plenum</i> (Lea, 1840)
<i>Proptera alata</i> (Say, 1817)	<i>Potamilus alatus</i>	<i>Potamilus alatus</i>
<i>P. laevisissima</i> (Lea, 1830)	<i>P. ohioensis</i> (Rafinesque, 1820)	<i>P. ohioensis</i> (Rafinesque, 1820)
<i>Ptychobranchus fasciolaris</i> (Rafinesque, 1820)		<i>Ptychobranchus fasciolaris</i>
<i>P. subtentum</i> (Say, 1825)		<i>P. subtentum</i>
<i>Quadrula cylindrica</i> (Say, 1817)		<i>Quadrula cylindrica</i>
<i>Q. cylindrica strigillata</i> (Wright, 1898)		<i>Q. cylindrica strigillata</i>
		<i>Q. fragosa</i> (Conrad, 1835)
<i>Q. intermedia</i> (Conrad, 1836)		<i>Q. intermedia</i>
<i>Q. metanevra</i> (Rafinesque, 1820)		<i>Q. metanevra</i>
		<i>Q. nodulata</i> (Rafinesque, 1820)
<i>Q. pustulosa</i> (Lea, 1831)	<i>Quadrula bullata</i> (Rafinesque, 1820)	<i>Q. pustulosa</i>
<i>Q. quadrula</i> (Rafinesque, 1820)		<i>Q. quadrula</i>
		<i>Q. sparsa</i> (Lea, 1841)

Table 1. (continued)

Bickel (1968)	Morrison (1969)	Taxonomy used in this study
<i>Simpsoniconcha ambigua</i> (Say, 1825)		<i>Simpsonaias ambigua</i>
<i>Strophitus rugosus</i> (Swainson, 1822)		<i>Strophitus undulatus</i> (Say, 1817)
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)		<i>Tritogonia verrucosa</i>
<i>Truncilla donaciformis</i> (Lea, 1828)		<i>Truncilla donaciformis</i>
<i>T. truncata</i> Rafinesque, 1820	<i>Truncilla vermiculata</i> (Rafinesque, 1820)	<i>T. truncata</i>
<i>Uniomerus tetralasmus</i> (Say, 1831)		<i>Uniomerus tetralasmus</i>
<i>Villosa fabalis</i> (Lea, 1831)		<i>Villosa fabalis</i>
<i>V. lienosa</i> (Conrad, 1834)		<i>V. lienosa</i>
<i>V. nebulosa</i> (Conrad, 1834)		<i>V. iris</i> (Lea, 1830)
<i>V. picta</i> (Lea, 1834)		<i>V. taeniata picta</i> (Lea, 1834)
	<i>Villosa teneltus</i> (Rafinesque, 1831)	<i>V. taeniata punctata</i> (Lea, 1865)
<i>V. taeniata</i> (Conrad, 1834)		<i>V. taeniata taeniata</i>
<i>V. trabalis</i> (Conrad, 1834)		<i>V. trabalis</i>
<i>V. trabalis perpurpurea</i> (Lea, 1861)		<i>V. perpurpurea</i>
<i>V. vanuxemensis</i> (Lea, 1838)		<i>V. vanuxemensis</i>

this analysis, we have included three additional Rafinesque species. Use of taxa originally described by Rafinesque is perceived as controversial due to their convoluted nomenclatural history (Bogan, Williams and Starnes, unpub. data).

FACTORS AFFECTING DISTRIBUTION OF UNIONIDS BY RIVER SYSTEM

MISSISSIPPI RIVER

The nature and size of the Mississippi River along the western border of Tennessee virtually precludes a diverse mollusk fauna. The river elevation annually fluctuates an average of 6 m between winter highs and summer lows. The substratum in shoal areas is sand and gravel while in pools it consists of shifting sand and mud. With few species recorded from the Mississippi River proper, most have come from oxbow lakes or tributary confluences.

Mississippi River tributaries in west Tennessee, with migratory fishes providing the mechanism for dispersal, would be expected to be relatively speciose. Unfortunately, agricultural development of deep soils formed in loess and the resulting deposition of sediments led to channelization of these tributary rivers (Forked Deer, Obion, Wolf and Loosahatchie) prior to documentation of their mussel fauna.

The Hatchie River (Table 2) appears to contain the only extant unionid fauna in Mississippi River tributaries in Tennessee. Due to its relatively uniform sand/silt substratum, diversity is relatively low in the Hatchie River. This limitation of habitat diversity is typical of direct Mississippi River tributaries. Most species recorded in the Hatchie River (D. Manning, pers. comm.) occur in the Tennessee and Cumberland rivers; six species are new to the state list: *Plectomerus dombeyanus* (Valenciennes, 1833), *Uniomerus declivis* (Say, 1831), *Toxolasma texasensis* (Lea, 1857), *Obovaria jacksoniana* (Frierson, 1912), *Potamilus purpurata* (Lamarck, 1819) and *Villosa vibex* (Conrad, 1834). Species such as *Plectomerus dombeyanus* are widespread in Gulf Coast streams.

TENNESSEE RIVER

A total of 126 mussel taxa occur in the Tennessee River and its tributaries. The Tennessee River, encompassing a watershed of over 105,000 km², has been divided into upper tributaries (Table 3) and middle and lower tributaries (Table 4).

The French Broad and Holston rivers join to form the Tennessee River. The Clinch and Powell rivers, originating in the Ridge and Valley Province in southwestern Virginia, flow into the Tennessee River. The underlying geology is folded and faulted Paleozoic limestone lying in parallel northeast-southwest ridges. Stream substrata are gravel, rubble and bedrock of primarily limestone (Fenneman, 1938). Water is hard and there are abundant nutrients [USEPA (United States Environmental Protection Agency) STORET Database]. The 45 taxa that Ortman (1924) considered "Cumberlandian" have been recorded in this physiographic province.

The eastern headwater tributaries of the Tennessee River arise in the Blue Ridge Province. The Watauga, Nolichucky, French Broad, Pigeon, Little, Little Tennessee and Hiwassee rivers originate along the western crest of the Blue Ridge (600-800 m). Except in lower reaches, streams are precipitous with soft water and low amounts of nutrients. Geologically, the area is comprised of metamorphosed sedimentary rocks, gneisses and schists (Fenneman, 1938). Boulders, cobbles and siliceous rocks are typical substrata. While there are endemic fish species such as brook trout [*Salvelinus fontinalis* (Mitchill)] in the Blue Ridge Province, "Cumberlandian" unionid species are rare or totally absent. Molluscan diversity and density, with few exceptions, increases after these streams enter the Ridge and Valley Province, lose gradient and change water chemistry (Bogan and Starnes, 1983).

The Emory River (Table 3), a tributary to the lower Clinch River, is a major stream draining the eastern portion of the Cumberland Plateau. The Emory River crosses geological strata that are characterized by Pennsylvanian sandstone, shale and coal. The substratum is sandy with

Table 2. List of Tennessee unionids found in the Mississippi River tributaries in Tennessee (N = Post 1960; R = Prior to 1960).

Species	North Fork Obion River	Reelfoot Lake	Hatchie River	Loosa- hatchie River	Wolf River	Horn Lake
<i>Amblema plicata</i>	R	R	N	R		
<i>A. plicata plicata</i>	R					
<i>Anodonta grandis</i>		R	N			
<i>A. grandis corpulenta</i>		R	N			
<i>A. imbecillis</i>		R	N			
<i>A. suborbiculata</i>		R	N		R	
<i>Arcidens confragosus</i>	R	R	N			
<i>Elliptio crassidens</i>				R		
<i>Fusconaia ebena</i>	R		N			
<i>F. flava</i>	R		N			
<i>F. flava trigona</i>	R					
<i>Lampsilis cardium satura</i>	R		N			
<i>L. siliquoidea</i>		N				
<i>L. teres teres</i>	R		N	R	R	
<i>L. teres anodontoides</i>			N			
<i>Lasmigona complanata</i>	R		N			
<i>Leptodea fragilis</i>		R	N		R	
<i>Ligumia subrostrata</i>		R	N			
<i>Megaloniais nervosa</i>	R	R	N			
<i>Obovaria jacksoniana</i>			N			
<i>Plectomerus dombeyanus</i>	R	R	N			
<i>Plethobasus cyphus</i>			N			
<i>Pleurobema cordatum</i>			N			
<i>Potamilus ohioensis</i>			N			
<i>P. purpurata</i>			N	R	R	
<i>Quadrula pustulosa</i>		R	N	R		
<i>Q. pustulosa mortoni</i>	R				R	
<i>Q. quadrula</i>	R	R	N	R		
<i>Strophitus undulatus</i>			N			N
<i>Toxolasma parva</i>		R	N			
<i>T. texasensis</i>		R	N			
<i>Tritogonia verrucosa</i>	R		N	R	R	
<i>Truncilla truncata</i>	R	R	N			
<i>Uniomerus declivis</i>			N			
<i>U. tetralasmus</i>			N			
<i>Villosa lienosa</i>			N			
<i>V. vibex</i>			N			
TOTAL TAXA	13	16	32	7	6	1

boulders, bedrock and shale. The water is soft, slightly acidic and nutrient limited. A total of 22 taxa, including 11 Cumberlandian endemics, have been recorded in this drainage, but most occur in the lower reaches when the river enters the Ridge and Valley Province and where the gradient has decreased. The Sequatchie River, a southward flowing tributary of the Tennessee River, drains the Southern Cumberland Plateau. Twenty unionid species are listed from the Sequatchie River (Table 4).

The Highland Rim Province dominates middle Tennessee and encompasses several major tributaries of the Tennessee River. Tributaries draining the crest of the Highland Rim from the south, elevations of 250-300 m, include the Elk, Flint and the Paint Rock rivers (the latter two do not contribute taxa to the Tennessee fauna). The Buffalo River drains the

interior of the southwestern Highland Rim while the Duck River drains the eastern and western rim as well as the southern Nashville Basin. These rivers are moderate in gradient, nutrient enriched and have hard water. Substrata consist of loose gravel or chert with limestone bedrock. Typically, these rivers are speciose with the Duck River (Table 4) having 69 taxa; 25 Cumberlandian species inhabit the upper Duck River. The Elk River (Table 4) similarly has 61 taxa recorded from its waters. The Buffalo River (Table 4), a tributary to the Duck River, is problematic; historically 27 taxa have been recorded from this river (van der Schalie, 1973) but few species have been recently collected in the drainage (Ahlstedt, 1986). This is despite the fact that water quality appears acceptable and faunal exchange could have occurred with the Tennessee or Duck rivers since the substratum appears very similar to

Table 3. Mollusks of the Upper Tennessee River and its headwater tributaries (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Clinch River	Emory River	Watauga River	French Broad River	Holston River	Little River	Nolichucky River	Powell River	Tenn. River
<i>Actionaias ligamentina</i>	RN				N		N	N	
<i>A. ligamentina gibba</i>	RNA			R	RN		RN	RN	R
<i>A. pectorosa</i>	RN		R		R	R	R	RN	R
<i>Alasmidonta ravenelina</i>					N				
<i>A. marginata</i>	RN		R		RN		N	RN	R
<i>A. viridus</i>	R			R	R	R			
<i>Amblyma plicata</i>	RNA	R		R	RN	R	RN	RN	R
<i>Anodonta grandis grandis</i>	N								
<i>A. grandis corpulenta</i>				R					
<i>A. suborbiculata</i>	N								
<i>Cumberlandia monodonta</i>	RN				R	R	RN	R	R
<i>Cyclonaias tuberculata tuberculata</i>	RNA			R	RN		RN	N	R
<i>Cyprogenia stegaria</i>	RNA				R			R	R
<i>Dromus dromas dromas</i>	NA				R			N	R
<i>D. dromas caperatus</i>	R				R			RN	R
<i>Ellipsaria lineolata</i>	R								R
<i>Elliptio crassidens</i>	RNA	R		R	RN		RN	RN	R
<i>E. dilatata</i>	RNA	RN	R	R	RN	N	RN	RN	R
<i>E. dilatata subgibbosus</i>	R								
<i>Epioblasma arcaeformis</i>	RA			R	R				R
<i>E. biemarginata</i>	R				R				
<i>E. brevidens</i>	RN				R			R	R
<i>E. capsaeformis</i>	RNA			R	R	N	RN	RN	R
<i>E. fiorentina</i>	RA			R					
<i>E. fiorentina walkeri</i>					R				
<i>E. haysiana</i>	RA				R	R		R	R
<i>E. lenior</i>	R				R				R
<i>E. lewisi</i>	R				R			R	R
<i>E. obliquata</i>	A								
<i>E. propinqua</i>	RA				R				R
<i>E. stewardsoni</i>	RA				R				R
<i>E. torulosa</i>									R
<i>E. torulosa gubernaculum</i>	RNA				R		R	R	
<i>E. triquetra</i>	RNA				R	R	RN	RN	R
<i>E. turgidula</i>	R	R		R	R				
<i>Fusconaia barnesiana</i>	RNA			R	R	RN	N	RN	R
<i>F. barnesiana bigbyensis</i>	RN		R	R	R	R		R	R
<i>F. barnesiana tumescens</i>	R	R		R	R				R
<i>F. cor analoga</i>	R				R			RN	
<i>F. cor</i>	RN							N	R
<i>F. cuneolus appressa</i>	R				R	RN	R		R
<i>F. cuneolus cuneolus</i>	NR	R			R			RN	R
<i>F. subrotunda</i>	RN		R		R		N	RN	
<i>F. subrotunda lesuerianus</i>	RN		R	R			R	R	R
<i>F. subrotunda pilaris</i>	R			R	R				R
<i>Hemistena lata</i>	RN				R			N	R
<i>Lampsilis abrupta</i>	RNA				R				R
<i>L. cardium</i>	R	R		R	R	RN	R	R	
<i>L. fasciola</i>	RNA	R	R	R	RN	RN	N	RN	R
<i>L. ovata</i>	RNA		N		RN		N	RN	R
<i>L. virescens</i>	R	R							
<i>Lasmigona complanata</i>					N				
<i>L. costata</i>	RN	R	R	R	R	N	N	RN	R
<i>L. holstonia</i>	R		R	R	R	R	R	R	R
<i>Lemiox rimosus</i>	RNA				R			RN	R
<i>Leptodea fragilis</i>	RN	N			RN		R	RN	R
<i>L. leptodon</i>	R				R				R
<i>Lexingtonia dolabelloides</i>	RNA			R				N	R

Table 3. (continued)

Species	French								
	Clinch River	Emory River	Watauga River	Broad River	Holston River	Little River	Nolichucky River	Powell River	Tenn. River
<i>L. dolabelloides conradi</i>	R				R				
<i>Ligumia recta</i>	RNA			R	RN		RN	RN	R
<i>L. recta latissima</i>	RN							R	
<i>Medionidus conradicus</i>	RN	R	R		R	RN		RN	R
<i>Obliquaria reflexa</i>	R				R				R
<i>Obovaria retusa</i>	R				R				R
<i>O. subrotunda subrotunda</i>	AR				R				R
<i>O. subrotunda lavigata</i>					R				
<i>Pegias fabula</i>				R	R				
<i>Plethobasus cicatricosus</i>	A				R				
<i>P. cooperianus</i>	RA			R	R				R
<i>P. cyphus</i>	RNA			R	RN			RN	R
<i>P. cyphus compertus</i>				R					R
<i>Pleurobema catillus</i>	R				R				
<i>P. clava</i>	A								
<i>P. coccineum</i>	R				R				
<i>P. cordatum</i>	RNA			R	RN		N		R
<i>P. oviforme</i>	RN	R		R	R			RN	R
<i>P. oviforme argenteum</i>	R		R	R	A	RN		R	
<i>P. oviforme holstonse</i>	R	R		R	R				R
<i>P. plenum</i>	RNA			R	R				R
<i>P. rubrum</i>	RNA			R	R				R
<i>Potamilus alatus</i>	RN	N		R	RN		RN	RN	R
<i>Ptychobranthus fasciolaris</i>	RNA	RN		R	R		N	RN	R
<i>P. subtentum</i>	RNA				R			RN	R
<i>Quadrula cylindrica cylindrica</i>	RNA				R			RN	R
<i>Q. cylindrica strigulata</i>	R				R			R	
<i>Q. intermedia</i>	RA				R		R	N	R
<i>Q. metanevra</i>	RNA				R				R
<i>Q. pustulosa</i>	RNA	N		R	RN		RN	RN	R
<i>Q. sparsa</i>	AN				R			N	
<i>Strophitus undulatus</i>	RN		RN	R	R			RN	R
<i>Toxolasma cylindrellus</i>				R					
<i>T. lividus glans</i>	R	RN				R			
<i>T. lividus lividus</i>	R	R		R	R			R	R
<i>T. parva</i>	R								
<i>Truncilla truncata</i>	RN				R		N		R
<i>Villosa fabalis</i>	R				R		R	R	R
<i>V. iris</i>	RN	R	R	R	R	RN	R	RN	R
<i>V. trabalis</i>	RA								
<i>V. perpurpurea</i>	RN	R			R				
<i>V. vanuxemensis</i>	RNA	R	R	R	R	RN	RN	RN	R
TOTAL TAXA	88	22	15	40	79	20	30	48	63

those rivers.

In addition to geology/water quality apparently affecting mussel diversity and abundance, there is a strong correlation between river drainage size and the occurrence of mussels. In the Tennessee River, the smallest tributary to have a diverse mussel fauna was Copper Creek (in Virginia) with 344.5 km² of watershed (Ahlstedt, 1982). Other streams with mussels had over 77.2 km² in drainage area.

SUMMARY OF TENNESSEE RIVER

The Tennessee River and its tributaries dominate the state. A total of 126 mussel taxa has been reported from the

Tennessee River drainage. This diversity is related to the geology of the area where the headwater tributaries of the river originate. The limestone enriched provinces of the headwater drainages provide an ideal scenario for an expanded mussel fauna: habitat diversity, abundant nutrients and calcium enriched (hard) water. Due to man-induced habitat changes (e.g. pollution and impoundments), the extant fauna in the State is largely restricted to four Tennessee River tributaries (i.e. the Duck, Elk, Clinch and Powell rivers). Construction of the Columbia Reservoir on the Duck River began in 1973 but was essentially halted in 1977. If that impoundment is completed, available habitat for Cumberlandian

mussel species will be further restricted by 32-48 km.

CUMBERLAND RIVER

The Cumberland River (Fig. 1) originates in the Cumberland Mountain subprovince of the Cumberland Plateau in southeastern Kentucky. It extends 1,105 km and has a drainage of 48,000 km². The Cumberland Plateau is underlain by Pennsylvanian strata consisting of alternating layers of shale, sandstone and coal. Water is soft and low in dissolved nutrients. While the upper Cumberland River is confined to Kentucky, the Big South Fork of the Cumberland River, a major tributary, drains the western Cumberland Plateau in Tennessee. Tributaries to the upper Cumberland River (Little South Fork of the Cumberland, Rockcastle and Laurel rivers) flow through Pennsylvanian-age strata through most of their drainage. The Big South Fork has eroded through Pennsylvanian into Mississippian strata (limestone). Twenty-five unionid species have been recorded from the Big South Fork drainage in Tennessee (Table 5).

As the Cumberland River enters Tennessee from Kentucky it is joined by the Wolf, Obey and Roaring rivers. These drain the eastern Highland Rim and possess substrata and water chemistry similar to the Duck and Buffalo rivers. The Obey River has 30 unionid species while the Roaring River (Table 5) has 7 species.

As the Cumberland River enters the Nashville Basin, it has reduced gradient and meanders westward across the Basin until it re-enters the western Highland Rim. From the south, the Cumberland River receives drainage from the Caney Fork River (southeastern Highland Rim) as well as the Stones River (central Nashville Basin) (Schmidt, 1982). The fauna of the Caney Fork (Table 5) is substantially reduced due to a waterfall below the confluence of the Collins and Rocky rivers. The Caney Fork River has 14 unionid taxa while the Stones River (Table 5) has 49 taxa.

After re-entering the Highland Rim, the Cumberland River flows westward through a deep alluvial floodplain. It receives several major tributaries draining the surrounding Highland Rim including the Harpeth and Red rivers and Yellow Creek (Table 5). These tributaries have upland characteristics with predominately chert-gravel substrata. The Harpeth and Red rivers have 25 and 22 taxa, respectively (Table 5).

SUMMARY OF CUMBERLAND RIVER

A total of 85 mussel taxa has been recorded from the Cumberland River and its tributaries in Tennessee. With 126 taxa recorded from the Tennessee River, this means that numerous taxa including Cumberlandian species *Quadrula sparsa* (Lea, 1841), *Lemiox rimosus* Rafinesque, 1831 and *Lexingtonia dolabelloides* (Lea, 1840) are absent from the Cumberland River. All of the mussel species recorded from the Cumberland River occur in the Tennessee River system.

The cause for this difference in total number of species is probably related to geology. The Cumberland River headwaters are in the nutrient-poor Pennsylvanian strata of the Cumberland Plateau. These tributaries have relatively depauperate faunas. It is only when streams cut through Pennsylvanian strata into limestone that diversity increases

(Starnes and Bogan, 1982). A comparison of fauna in the Tennessee and Cumberland rivers reveals that primarily the headwater-mussel species are absent from the Cumberland River. Thus, while these two rivers seem similar physiographically, they are discretely different and this translates into a slightly different mussel fauna.

CONASAUGA RIVER

This tributary to the Coosa River originates in the Blue Ridge Province of northern Georgia and southern Tennessee. The geology of the area is dominated by granite, gneisses, schists and metamorphic rocks (Fenneman, 1938) that produce soft water with low nutrients. Mussels are absent from this headwater area. After the river enters the Coosa Valley (Ridge and Valley) Province, water becomes hard, nutrients increase and bivalves begin to appear. The Conasauga River in Tennessee contains 27 taxa (Table 6). Of these, *Elliptio dilatata* (Rafinesque, 1820), *Anodonta grandis corpulenta* Cooper, 1834, *A. imbecillus* Say, 1829, *Lasmigona holstonia* (Lea, 1838), *Toxolasma parva* (Barnes, 1823), *Medionidus conradicus* (Lea, 1834), *Villosa lienosa* (Conrad, 1834) and *V. vanuxemensis* (Lea, 1838) also occur in the Tennessee/Cumberland rivers and/or their tributaries. The remaining 19 taxa are additions to the state species list and are typical of the Coosa River system and Gulf coast streams (Table 6).

Near the Tennessee/Georgia border unionid species diversity increases. An additional 15 species were collected by Hurd (1974) immediately below that border but have not been collected in Tennessee. These additional species may be limited by habitat diversity or stream size from expanding further upstream in the Conasauga River. Further research into this area could be useful in understanding factors restricting mussel distributions.

DISCUSSION

The earliest unionid faunal descriptions in Tennessee were in the early 1800s. Subsequent malacological work has tended to investigate the same rivers with diverse unionid faunas while ignoring other major streams. It is ironic that no comprehensive faunal surveys have been completed, until recently, on the Conasauga, Hatchie or Mississippi rivers and tributaries in Tennessee. Other works, such as ecological studies of endemic species, are also very limited.

Since Ortmann's work (1918, 1924, 1925) on the Tennessee River system, rivers in this State have undergone considerable change. There are now nine reservoirs on the main Tennessee River, making it essentially a series of impoundments from its origin near Knoxville to its confluence with the Ohio River. While the lack of complete historical data on the early abundance and diversity of molluscan populations in the Tennessee River (Table 6) and its tributaries confounds any efforts to estimate the impact from man-made alterations, changes have taken place. We can neither quantify the change that has occurred in mussel populations during historical times nor can we reliably predict what previous changes portend for the health and survival of existing populations.

Table 4. Mollusks of the Middle and Lower Tennessee River and major tributaries (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Middle Tennessee River				Lower Tennessee River			
	Little Tenn. River	Hiwassee River	Squatchie River	Tenn. River	Elk River	Duck River	Buffalo River	Tenn. River
<i>Actionaias ligamentina</i>				A	NR	RN	RN	
<i>A. ligamentina gibba</i>	NA			RN				RN
<i>A. pectorosa</i>			R		RNA	RN	R	
<i>Alasmidonta marginata</i>	N				R	RN	R	
<i>A. viridus</i>		R	R		R	RN	R	
<i>Amblema plicata</i>	NA		R	RNA	RN	RNA		RN
<i>Anodonta grandis</i>	NA			N	NR	RN		N
<i>A. grandis corpulenta</i>				N				
<i>A. imbecillis</i>						R		RN
<i>A. suborbiculata</i>								N
<i>Arcidens confragosus</i>								N
<i>Cumberlandia monodonta</i>			R					N
<i>Cyclonaias tuberculata</i>	NA		R	RNA	RN	RNA	RN	N
<i>C. tuberculata granifera</i>				N				RN
<i>Cyprogenia stegaria</i>	A			RNA		R		N
<i>Dromus dromas</i>	A			RNA	NR			
<i>Ellipsaria lineolata</i>				RN	NR	R		RN
<i>Elliptio crassidens</i>	NA	R	R	RNA	N	RN		RN
<i>E. dilatata</i>	RNA		R	RNA	RNA	RNA		RN
<i>Epioblasma arcaeiformis</i>	A			A				
<i>E. biemarginata</i>			R		R			
<i>E. brevidens</i>	A			A	R	RN		
<i>E. capsaeformis</i>	RA			A	RNA	RNA		
<i>E. flexuosa</i>				A				
<i>E. florentina</i>	R			A	RN	A		
<i>E. florentina walkeri</i>						R	R	
<i>E. haysiana</i>	RA			A	R			
<i>E. lenior</i>						R		
<i>E. lewisi</i>						A		
<i>E. obliquata</i>				A				
<i>E. propinqua</i>	A			A				
<i>E. stewardsoni</i>	A			A				
<i>E. torulosa</i>	A			RA	RN	R		
<i>E. triquetra</i>				A	RN	RNA		
<i>E. turgidula</i>				A	R	R		
<i>Fusconaia barnesiana</i>	RNA	R	R	A	RNA	RNA	RN	
<i>F. barnesiana bigbyensis</i>	R	R			R	R	R	
<i>F. barnesiana tumescens</i>	R	R						
<i>F. cor</i>					RN			
<i>F. cuneolus</i>					RN			
<i>F. cuneolus appressa</i>								
<i>F. ebena</i>				N				RN
<i>F. flava</i>								N
<i>F. subrotunda</i>	RNA			NA	RN			RN
<i>Hemistena lata</i>					RN	R	R	N
<i>Lampsilis abrupta</i>	N			N				RN
<i>L. cardium</i>					R	R	R	R
<i>L. fasciola</i>	RNA		R	RNA	RNA	RNA	R	
<i>L. ovata</i>	RNA			NA	NA	RNA		N
<i>L. teres anodontoides</i>						RN		RN
<i>L. teres teres</i>					N			RN
<i>Lasmigona complanata</i>				N	N	RN	R	
<i>L. costata</i>			R	RA	RN	RN	R	
<i>L. holstonia</i>		R		R		R		
<i>Lemiox rimosus</i>	A			A	RN	RNA		
<i>Leptodea fragilis</i>	N		R	N	RN	RN	RN	N
<i>L. leptodon</i>						R		

Table 4. (continued)

Species	Middle Tennessee River			Lower Tennessee River				
	Little Tenn. River	Hiwassee River	Sequatchie River	Tenn. River	Elk River	Duck River	Buffalo River	Tenn. River
<i>Lexingtonia dolabelloides</i>	NA			RA	RNA	RNA		N
<i>L. dolabelloides conradi</i>						R	R	
<i>Ligumia recta</i>	NA			NA				N
<i>L. recta latissima</i>				N		RN		R
<i>Medionidus conradicus</i>	NA				RNA	RNA		
<i>Megalonaias nervosa</i>				N	RN	RN		RN
<i>Obliquaria reflexa</i>				RN	RN	RN		RN
<i>Obovaria olivaria</i>				N				RN
<i>O. retusa</i>	A			A		R		RN
<i>O. subrotunda</i>	A			A	N	RNA	R	
<i>O. subrotunda lens</i>			R		RN	R	R	
<i>Pegias fabula</i>				RA	RA			
<i>Plethobasus cicatricosus</i>				A				
<i>P. cooperianus</i>	A			RA		N		RN
<i>P. cyphus</i>	NA			NA				RN
<i>Pleurobema catillus</i>						R		
<i>P. clava</i>			R	A				
<i>P. cordatum</i>	NA			RNA	N	RN		RN
<i>P. oviforme</i>	RNA	R			RNA	RNA	R	
<i>P. oviforme holstonse</i>	R	R		R		R		
<i>P. oviforme argenteum</i>		R			R	R	R	
<i>P. plenum</i>	A			RA				R
<i>P. rubrum</i>	NA			RNA		NR		R
<i>P. coccineum</i>	A							R
<i>Potamilus alatus</i>	NA		R	RNA	N	RN		RN
<i>P. ohioensis</i>	R					N	N	
<i>Ptychobranthus fasciolaris</i>	A			RNA	RNA	RN		RN
<i>P. subtentum</i>	A			A	RNA	RA	R	
<i>Quadrula cylindrica</i>	A		R	A	RNA	RNA		
<i>Q. fragosa</i>						R		RN
<i>Q. intermedia</i>				A	RN	RN		
<i>Q. metanevra</i>	NA			RNA	RN			RN
<i>Q. nodulata</i>								N
<i>Q. pustulosa</i>	NA			RNA	N	RN		RN
<i>Q. quadrula</i>					N	RN		RN
<i>Q. sparsa</i>	R			A				
<i>Strophitus undulatus</i>	N			A	RNA	RNA	R	
<i>Toxolasma cylindrellus</i>			RN		R	R	R	
<i>T. lividus glans</i>					N	RN		
<i>T. parva</i>				R				
<i>Tritogonia verrucosa</i>		R		N	RN	RN		RN
<i>Truncilla donaciformis</i>				N	N	RN		RN
<i>T. truncata</i>					N	RN		R
<i>Uniomerus tetralasmus</i>								N
<i>Villosa fabalis</i>					N	RN		
<i>V. iris</i>	R	R	R	R	RN	RNA	RN	
<i>V. taeniata</i>					RNA	RNA	RN	
<i>V. trabalis</i>		R						
<i>V. vanuxemensis</i>		RNA	R	A	RNA	RNA	RN	
TOTAL TAXA	50	12	20	66	61	68	27	45

ARCHAEOLOGICAL RECORD

The archaeological record is a valuable resource in documenting the historical unionid fauna of Tennessee and can provide clues to the early historical abundance and

distribution of mussel populations. It provides malacologists with a significant supplement to historical mollusk collections. The archaeological record can provide insight into the former unionid fauna of what is now a dead or severely altered river

(e.g. van der Schalie and Parmalee, 1960) or the past distribution of species not documented in historic collections (e.g. Parmalee *et al.*, 1980).

Parmalee and Bogan (1986) discuss the late prehistoric bivalve fauna of the lower Clinch River and document an archaeological assemblage richer and more diverse than that reported by Ortmann (1918). The diverse prehistoric fauna of the main channel of the Tennessee River in East Tennessee has been alluded to by Parmalee (1966), Charles (1973) and Bogan and Parmalee (1977). Parmalee *et al.* (1982) document the past unionid diversity of the Tennessee River above Chattanooga, reporting 45 species from a series of archaeological shell middens. They observed a major shift in the species composition from late prehistoric samples to that fauna represented in reaches impounded since the 1940's. For example, the most common species identified in these archaeological samples was *Dromus dromas* (Lea, 1834), an endangered species (see Bogan and Parmalee, 1983) almost extirpated from the main Tennessee River. The relative dominance of *Dromus* in the prehistoric samples from the Chickamauga Reservoir is comparable to those archaeological assemblages from Widow's Creek in northern Alabama (Warren, 1975) and the large samples reported by Morrison (1942) from the Pickwick Landing basin along the middle stretch of Tennessee River in northwestern Alabama. The relative abundance of the rest of the species is comparable within the archaeological samples from the Clinch River, Chickamauga Reservoir and the two Alabama studies. These archaeological assemblages, when compared with the present fauna, point to some major shifts in species assemblages and abundance over the last 180 years. There has been almost complete extirpation of all species of big river *Epioblasma* sp. as well as other taxa such as *Plethobasus cooperianus* (Lea, 1834), *Actinonaias ligamentina* (Lamarck, 1819), *Quadrula intermedia* (Conrad, 1836), *Cyprogenia stegaria* (Rafinesque, 1820), *Obovaria retusa* (Lamarck, 1819) and *Pleurobema clava* (Lamarck, 1819). These species have been replaced by other taxa such as *Ellipsaria lineolata* (Rafinesque, 1820), *Obliquaria reflexa* Rafinesque, 1820, *Tritogonia verrucosa* (Rafinesque, 1820), *Megalonaias nervosa* (Rafinesque, 1820) and *Anodonta* spp., which were essentially absent from the archaeological record.

The naiad fauna of the Little Tennessee River, a tributary of the Tennessee River in East Tennessee, was surveyed and reported by Tennessee Valley Authority (1972) as having a fauna of about 20 unionid species. Bogan (1982) summarized the late prehistoric and early historic unionid fauna of the Little Tennessee River as reported by Bogan (1978, 1980, 1983), Robison (1978) and Bogan and Bogan (1985), and had consisted of 46 species; an additional 14 species were expected but not found in the archaeological samples. This reconstruction of the early historic fauna compares favorably with other documented historic naiad faunas from the Clinch, Holston and/or Powell rivers (Ortmann, 1918).

Archaeological bivalves recovered from the Eva site on the west bank of the Tennessee River downstream from the mouth of the Duck River document the former occurrence of at least some of the "Cumberlandian" species as far

downstream as the mouth of the Duck River. Casey (1986) documented the prehistoric occurrence of two Cumberlandian species [*Epioblasma arcaeiformis* (Lea, 1831), *Dromus dromas*] near the mouth of the Tennessee River (River Mile 17.4) and the Cumberland River (River Mile 26) in Kentucky. Parmalee (1982) and Parmalee and Klippel (1986) reported the former occurrence of at least 26 species in the Duck River based on a sample of naiads recovered from early and mid-Holocene deposits. Robison (1986) included a discussion of aboriginal unionid samples from the Duck and upper Elk rivers.

Ortmann (1926b), in discussing the unionid fauna of the Green River in Kentucky, noted the absence of *Epioblasma torulosa* (Rafinesque, 1820) from the Cumberland River (excluding a probably spurious record from Walker). However, Parmalee *et al.* (1980) compared the modern fauna of the Cumberland River with archaeological samples and documented the former occurrence of *E. torulosa* in the Cumberland River and noted that it was a common species in the prehistoric faunal assemblage. Casey (1986) recorded specimens of the *E. torulosa* complex from these same sites.

These examples clearly exemplify the importance of archaeological material to the study of prehistoric and early historic unionid distributions. The archaeological record is an important supplement to modern collections and provides a historical perspective on some of the changes in the naiad fauna that have occurred in the past 180 years.

FAUNAL EXCHANGES

Evidence of faunal exchange between the Tennessee and Cumberland rivers and the Ozark Region is supported by archaeological records showing a larger range for "Cumberlandian" species than envisioned by Ortmann. Ortmann (1925) recognized that these two regions shared certain species, but did not elaborate. *Cumberlandia monodonta* (Say, 1829) and *Epioblasma turgidula* (Lea, 1848) are shared exclusively by these two regions. There is additional evidence of faunal affinities with closely related taxa [i.e. *Fusconaia barnesiana* (Lea, 1838) in the Tennessee and Cumberland rivers and *F. ozarkensis* (Call, 1887) in the Ozarks]. Similar affinities exist for *Ptychobranthus fasciolaris* (Rafinesque, 1820) and *P. occidentalis* (Conrad, 1836), and *Cyprogenia stegaria* (Rafinesque, 1820) and *C. alberti* (Conrad, 1850). The Tennessee and Cumberland river drainages share many upland fish species groups and subgenera with the Ozarkian region [for example: *Notropis galacturus* (Cope), *N. telescopus* (Cope), *Typhlichthys subterraneus* Girard and *Fundulus catenatus* (Storer) are exclusively shared by these regions (Starnes and Etnier, 1986)]. These two regions exclusively share fish and mussel species and yet these same species are absent from adjacent tributaries to the Mississippi or Ohio rivers.

Thus far, discussions of the Tennessee and Cumberland rivers have indicated that their mussel faunas are very similar. Ortmann (1925) reported 10 taxa that were known to be present in the Tennessee River but absent from the Cumberland River. Of the Cumberlandian species found in the Tennessee and Cumberland rivers, the following are absent from the lower Tennessee (Ortmann, 1924): *Quadrula*

Table 5. Species of the Cumberland River and its tributaries (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Cumber- land River	Big So. Fork Cumber- land River	Obey River	Caney Fork River	Stones River	Harpeth River	Red River	Roaring River
<i>Actinonaias ligamentina</i>	RNA		R		N	R		
<i>A. ligamentina gibba</i>	R			R			R	
<i>A. pectorosa</i>		N	R	R	N		R	
<i>Alasmidonta atropurpurea</i>		N		N				
<i>A. marginata</i>	R		NR				N	
<i>A. viridis</i>					N	N	N	
<i>Amblema plicata</i>	NA		R		RN			
<i>A. plicata perplicata</i>	R						R	
<i>A. plicata plicata</i>	N							
<i>Anodonta grandis</i>	RN				RN			
<i>A. imbecillis</i>	RN				RN			
<i>Anodontoides ferussacianus</i>	R							R
<i>Cumberlandia monodonta</i>	RN			R	N			
<i>Cyclonaias tuberculata</i>	RNA		R		N	R	R	
<i>C. tuberculata granifera</i>	R							
<i>Cyprogenia stegaria</i>	RNA							
<i>Dromus dromas</i>	RNA					R		
<i>Ellipsaria lineolata</i>	RN				N			
<i>Elliptio crassidens</i>	RNA	N	R				R	
<i>E. dilatata</i>	RNA	N	R		N	R	R	
<i>Epioblasma arcaeiformis</i>	A				R			
<i>E. brevidens</i>	NA	N		R	N			
<i>E. capsaeformis</i>	RA	?	R	R				
<i>E. flexuosa</i>	A							
<i>E. florentina</i>	RA		R		R	R	R	
<i>E. florentina walkeri</i>	RN		?		RN	R	R	
<i>E. havsiana</i>	RA							
<i>E. lenior</i>					RN			
<i>E. obliquata</i>	N			R		R		
<i>E. stewardsoni</i>	A							
<i>E. torulosa</i>	NA							
<i>E. triquetra</i>	N		R					
<i>Fusconaia ebena</i>	RN							
<i>F. flava</i>	RNA				RN	R		
<i>F. subrotunda</i>	RNA		R					
<i>Hemistena lata</i>	R	R						
<i>Lampsilis abrupta</i>	RNA		R					
<i>L. cardium</i>	R	N			RN	R		
<i>L. fasciola</i>	RA	N	R		RN	R	R	R
<i>L. ovata</i>	RNA	N	R	R	N		R	
<i>L. teres anodontoides</i>	RN		R		N	R	R	
<i>L. teres teres</i>	RN							
<i>Lasmigona complanata</i>	RN			R	RN	R	R	
<i>L. costata</i>	RNA	N	R	R	RN	R	R	R
<i>Leptodea fragilis</i>	RN				N			
<i>Lexingtonia dolabelloides</i>	NA							
<i>Ligumia recta latissima</i>	RNA	N	R		N	R		
<i>Medionidus conradicus</i>		N			RN			R
<i>Megalonaias nervosa</i>	RN				RN		R	
<i>Obliquaria reflexa</i>	RNA		R	R	N			
<i>Obovaria olivaria</i>	RN							
<i>O. retusa</i>	RNA							
<i>O. subrotunda</i>	RA		R		RN	R	RN	
<i>Pegias fabula</i>		N		RN	N			
<i>Plethobasus cicatricosus</i>	A			R				
<i>P. cyphyus</i>	RNA							
<i>P. cooperianus</i>	RNA							
<i>Pleurobema catillus</i>	R							

Table 5. (continued)

Species	Cumber- land River	Big So. Fork Cumber- land River	Obey River	Caney Fork River	Stones River	Harpeth River	Red River	Roaring River
<i>P. clava</i>	NA							
<i>P. cordatum</i>	RNA				N			
<i>P. gibberum</i>				N				
<i>P. oviforme</i>		N	R		N			
<i>P. plenum</i>	RNA							
<i>P. rubrum</i>	RNA				N			
<i>P. coccineum</i>	NA	N			N			
<i>Potamilus alatus</i>	RNA	N	R		N		R	
<i>P. ohioensis</i>	R					R		
<i>Ptychobranchnus fasciolare</i>	RNA	N	R		N		R	
<i>P. subtentum</i>		N	R	R		R		
<i>Quadrula cylindrica</i>	RNA		R		N			
<i>Q. fragosa</i>	RN					R		
<i>Q. metanevra</i>	RNA		R					
<i>Q. pustulosa</i>	RNA	N			N	R		
<i>Q. quadrula</i>	N				N			
<i>Simpsonaias ambigua</i>					N			
<i>Strophitus undulatus</i>	R	N	R		N	R	R	
<i>Toxolasma lividus glans</i>								R
<i>T. lividus lividus</i>					RN	?		
<i>T. parva</i>					N			
<i>Tritogonia verrucosa</i>	RN	N	R		N	R	R	
<i>Truncilla donaciformis</i>	R				N	R		
<i>T. truncata</i>	RN			R	N		R	
<i>Villosa iris</i>	A	N	R		N			
<i>V. lienosa</i>	R				N			
<i>V. taeniata picta</i>						R		R
<i>V. taeniata punctata</i>								R
<i>V. taeniata</i>	RNA	N	R	N	RN			
<i>V. trabalis</i>		N	RN					
<i>V. vanuxemensis</i>					N	?	R	
TOTAL TAXA	68	25	30	14	49	25	22	7

cylindrica strigillata (Wright, 1898); *Plethobasus cyphus comperatus* (Frierson, 1911); *Alasmidonta raveneliana* (Lea, 1834); *Villosa perpurpurea* (Lea, 1861); *Epioblasma torulosa gubernaculum* (Reeve, 1865); *E. stewardsoni* (Lea, 1852); *E. lewisi* (Walker, 1910). A total of 87 mussel taxa have been reported from the Cumberland River drainage while 126 taxa have been recorded from the Tennessee River drainage. Thus, while many species are shared, the fauna from the Cumberland River does not include every species present in the Tennessee River.

Faunal similarities occur between the two rivers because of habitat and geological similarities instead of faunal exchanges that would tend to make the faunas identical in at least those rivers/streams where the exchange occurred (see Starnes and Etnier, 1986). There are geological differences between the two river drainages. Among these, there is less physiographic diversity in the Cumberland River drainage with the tributaries originating in Pennsylvanian strata while those of the Tennessee River originate in Ridge and Valley strata. This geologic dissimilarity between the Tennessee and Cumberland tributaries probably contributes to

the dissimilarity in the total number of species. The Clinch River, a part of the upper Tennessee River system, has had 89 taxa reported from its drainage. In contrast, the Stones River, the tributary with the most diverse fauna in the Cumberland River system, had only 49 taxa reported.

FAUNAL ALTERATIONS

As stated earlier, man-made river alterations have affected mussel populations throughout recorded history. In impoundments the species *Anodonta grandis* Say, 1829; *A. imbecillis*; *A. suborbiculata* Say, 1831; *Obliquaria reflexa*; *Tritogonia verrucosa*; *Elliptio crassidens* (Lamarck, 1819) and *Quadrula quadrula* (Rafinesque, 1820) have expanded their populations and distribution. While these species have proliferated in reservoirs, those species requiring riverine environments for themselves or for their host fish species have disappeared. Riverine species associated with the lower Tennessee and Cumberland rivers appear least affected by impoundments, perhaps because there is little difference between a deep, slow-flowing river and a deep, slow-flowing impoundment.

Table 6. Mollusks tabulated by river system (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Tennessee River			Conasauga River	Cumberland River	Mississippi River Tributaries
	Upper	Middle	Lower			
<i>Actionaias ligamentina</i>	RN	A	RN		RNA	
<i>A. ligamentina gibba</i>	RN	RN	RN		R	
<i>A. pectorosa</i>	RN	R	RN		R	
<i>Alasmidonta atropurpurea</i>					N	
<i>A. marginata</i>	RN		RN		RN	
<i>A. viridus</i>	R	R	RN		N	
<i>Amblema plicata</i>					RNA	RN
<i>A. plicata perplicata</i>					R	
<i>A. plicata plicata</i>	RN	RNA	RN		RNA	RN
<i>Anodonta grandis</i>	RN	N	RN		RN	RN
<i>A. grandis corpulenta</i>	R			N		RN
<i>A. imbecillus</i>			RN	N	RN	RN
<i>A. suborbiculata</i>	N		N			Rn
<i>Anodontoides ferussacianus</i>					R	
<i>Arcidens confragosus</i>			N			RN
<i>Cumberlandia monodonta</i>	RN	R	NR		RN	
<i>Cyclonaias tuberculata</i>	RN	RNA	RN		RNA	
<i>C. tuberculata granifera</i>	N	N	RN		R	
<i>Cyprogenia stegaria</i>	RN	RNA	RN		RNA	
<i>Dromus dromas dromas</i>	RN	RNA	R		RNA	
<i>D. dromas caperatus</i>	R					
<i>Ellipsaria lineolata</i>	R	RN	RN		RN	
<i>Elliptio arcata</i>				N		
<i>E. crassidens</i>	RN	RNA	RN		RNA	R
<i>E. dilatata</i>	RN	RNA	RN	N	RNA	
<i>E. dilatata subgibbosus</i>	R					
<i>Epioblasma arcaeiformis</i>	R	A			RA	
<i>E. biemarginata</i>			R			
<i>E. brevidens</i>	RN	A	RN		RNA	
<i>E. capsaeformis</i>	RN	RA	RN		RA	
<i>E. flexuosa</i>		A			A	
<i>E. florentina</i>	R	A	N		RA	
<i>E. florentina walkeri</i>	R		RN			
<i>E. haysiana</i>	R	RA	R		RA	
<i>E. lenior</i>	R		R		N	
<i>E. lewisi</i>	R					
<i>E. metastrata</i>				N		
<i>E. obliquata</i>		A			RN	
<i>E. propinqua</i>	R	A				
<i>E. stewardsoni</i>	R	A			A	
<i>E. torulosa torulosa</i>	R	RA	R		NA	
<i>E. torulosa gubernaculum</i>	RN					
<i>E. triquetra</i>	RN	A	RN		N	
<i>E. turgidula</i>	R	A	RN			
<i>Fusconaia barnesiana barnesiana</i>	RN	RA	RN			
<i>F. barnesiana bigbyensis</i>	RN	R	R			
<i>F. barnesiana tumescens</i>	R	R	R			
<i>F. cor analoga</i>	R					
<i>F. cor cor</i>	RN		N			
<i>F. cuneolus cuneolus</i>			N			
<i>F. cuneolus appressa</i>	R					
<i>F. ebena</i>		N	RN		R	RN
<i>F. flava</i>			N		RN	RN
<i>F. flava trigona</i>						R
<i>F. subrotunda</i>	RN		N		RNA	
<i>F. subrotunda lesuerianus</i>	RN					
<i>F. subrotunda pilaris</i>	RN	RA	RN			

Table 6. (continued)

Species	Tennessee River			Conasauga River	Cumberland River	Mississippi River Tributaries
	Upper	Middle	Lower			
<i>Hemistena lata</i>	RN		RN		R	
<i>Lampsilis abrupta</i>	RN	N	RN		RNA	
<i>L. altilis</i>				N		
<i>L. cardium</i>	R	R	R		RN	
<i>L. cardium satura</i>						RN
<i>L. clarkiana</i>				N		
<i>L. fasciola</i>	RN	RNA	RN		RNA	
<i>L. ornata</i>				N		
<i>L. ovata</i>	RN	RNA	RN		RNA	
<i>L. siliquoidea</i>						N
<i>L. straminea claiborensis</i>				N		
<i>L. teres</i>			RN		RN	RN
<i>L. teres anodontoides</i>						N
<i>L. virescens</i>	R					
<i>Lasmigona complanata</i>	RN		RN		RN	RN
<i>L. costata</i>	RN	RA	RN		RNA	
<i>L. holstonia</i>	R	R	R	N		
<i>Lemiox rimosus</i>	RN	A	RN			
<i>Leptodea fragilis</i>	RN	RN	RN		RN	RN
<i>L. leptodon</i>	RN		R			
<i>Lexingtonia dolabelloides</i>	RN	RA	RN		NA	
<i>L. dolabelloides conradi</i>	R		R			
<i>Ligumia recta</i>	RN	NA	N			
<i>L. recta latissima</i>	RN	N	RN		RNA	
<i>L. subrostrata</i>						RN
<i>Medionidus acutissimus</i>				N		
<i>M. conradicus</i>	RN		RN	N	RN	
<i>Megaloniaias nervosa</i>		N	RN		RN	RN
<i>Obliquaria reflexa</i>	R	RN	RN		RNA	
<i>Obovaria jacksoniana</i>						N
<i>O. olivaria</i>		N	RN		RN	
<i>O. retusa</i>	R	A	RN		RNA	
<i>O. subrotunda</i>	R	A	RN		RNA	
<i>O. subrotunda levigata</i>	R					
<i>O. subrotunda lens</i>		R	RN			
<i>Pegias fabula</i>	R	R			N	
<i>Plectomerus dombeyanus</i>						RN
<i>Plethobasus cicatricosus</i>		A			RA	
<i>P. cooperianus</i>	R	RA	RN		RNA	
<i>P. cyphus</i>	RN	NA	RN		RNA	N
<i>P. cyphus compertus</i>	RN	NA	RN		RNA	N
<i>Pleurobema aldrichianum</i>				N		
<i>P. catillus</i>	R		R		R	
<i>P. clava</i>		RA			NA	
<i>P. cordatum</i>	RN	RNA	RN		RNA	N
<i>P. georgianum</i>				N		
<i>P. gibberum</i>					N	
<i>P. hanleyanum</i>				N		
<i>P. johannis</i>				N		
<i>P. oviforme</i>	RN	R	RN		N	
<i>P. oviforme holstonse</i>	R	R	R			
<i>P. oviforme argenteum</i>	RA		R			
<i>P. perovatum</i>				N		
<i>P. plenum</i>	RN	AN	R		RNA	
<i>P. rubellum</i>				N		
<i>P. rubrum</i>	RN	RA	R		RNA	
<i>P. coccineum</i>	R	R	R		NA	
<i>P. troschelianum</i>				N		

Table 6. (continued)

Species	Tennessee River			Conasauga River	Cumberland River	Mississippi River Tributaries
	Upper	Middle	Lower			
<i>Potamilus alatus</i>	RN	RNA	RN		RNA	
<i>P. ohioensis</i>			RN		N	RN
<i>P. purpurata</i>						RN
<i>Ptychobranchus fasciolaris</i>	RN	RNA	RN		RNA	
<i>P. greeni</i>				N		
<i>P. subtentum</i>	RN	A	RN		R	
<i>Quadrula cylindrica</i>	RN	RA	RN		RNA	
<i>Q. cylindrica strigulata</i>	R					
<i>Q. fragosa</i>			RN		RN	
<i>Q. intermedia</i>	RN	A	RN			
<i>Q. metanevra</i>	RN	RNA	RN		RNA	
<i>Q. nodulata</i>			N			
<i>Q. pustulosa</i>	RN	RNA	RN		RNA	RN
<i>Q. pustulosa mortoni</i>						RN
<i>Q. quadrula</i>			RN		N	RN
<i>Q. sparsa</i>	N					
<i>Simpsonaias ambigua</i>					N	
<i>Strophitus connasaugaensis</i>				N		
<i>S. undulatus</i>	RN	A	RN		RN	RN
<i>Toxolasma cylindrellus</i>			R			
<i>T. lividus glans</i>	R		RN	N	R	
<i>T. lividus lividus</i>	R				RN	
<i>T. parva</i>	R	R		N	N	RN
<i>T. texasensis</i>						RN
<i>Tritogonia verrucosa</i>		RN	RN		RN	RN
<i>Truncilla donaciformis</i>		N	RN		RN	
<i>T. truncata</i>	RN		RN		RN	RN
<i>Unio merus declivis</i>						N
<i>U. tetralasmus</i>						N
<i>Villosa fabalis</i>	R		RN			
<i>V. iris</i>	RNR	RN		N	NA	
<i>V. lienosa</i>				N	RN	N
<i>V. taeniata picta</i>	N?				R	
<i>V. taeniata punctata</i>					R	
<i>V. taeniata taeniata</i>			RN		RNA	
<i>V. trabalis</i>	R	R			R	
<i>V. trabalis perpurpurea</i>	RN					
<i>V. vanuxemensis</i>	RN	R	RNA	N	RN	
<i>V. vanuxemensis umbrans</i>				N		
<i>V. vibex</i>				N		N
TOTAL TAXA	94	73	89	27	85	35

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